



University of Groningen

A three-stage symbiosis forms the foundation of seagrass ecosystems

van der Heide, Tjisse; Govers, Laura L.; de Fouw, Jimmy; Olf, Han; van der Geest, Matthijs; van Katwijk, Marieke M.; Piersma, Theunis; van de Koppel, Johan; Silliman, Brian R.; Smolders, Alfons J. P.

Published in:
Science

DOI:
[10.1126/science.1219973](https://doi.org/10.1126/science.1219973)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2012

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van der Heide, T., Govers, L. L., de Fouw, J., Olf, H., van der Geest, M., van Katwijk, M. M., ... van Gils, J. A. (2012). A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science*, 336(6087), 1432-1434. <https://doi.org/10.1126/science.1219973>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.



Supplementary Material for

A Three-Stage Symbiosis Forms the Foundation of Seagrass Ecosystems

Tjisse van der Heide,* Laura L. Govers, Jimmy de Fouw, Han Olf,
Matthijs van der Geest, Marieke M. van Katwijk, Theunis Piersma, Johan van de Koppel,
Brian R. Silliman, Alfons J. P. Smolders, Jan A. van Gils

*To whom correspondence should be addressed. E-mail: t.van.der.heide@rug.nl

Published 15 June 2012, *Science* **336**, 1432 (2012)
DOI: 10.1126/science.1219973

This PDF file includes:

Materials and Methods

Supplementary Text

Figs. S1 to S4

Tables S1 and S2

References (29–119)

Materials and Methods.

Meta-analysis.

To test the seagrass-lucinid association, we performed an extensive, worldwide meta-analysis that covered the entire climatic distribution of seagrasses. Criteria for including a study were: (1) seagrasses were present at the site, and (2) when Lucinidae were present, they were found inside the seagrass bed. In total, we analyzed 84 studies that sampled the fauna of seagrass beds in a total of 83 areas (temperature range = 1 to 33 °C, mean = 22 °C). Overall, 36 sites were from tropical areas, 31 from subtropical and 16 from temperate areas; quantitative data were available for 46 out of 83 sites. Apart from the geographical location of each site, and the seagrass and lucinid families found, we also report the annual seawater temperature range. These were obtained from freely available satellite imagery of the long-term monthly means (1971 – 2000) of the sea surface temperature (29).

Field study.

We conducted a field survey at Banc d'Arguin (Mauritania) to test the strength of the relation between seagrass biomass and lucinid density. Banc d'Arguin consists of about 500 km² of intertidal flat dominated by mixed meadows of *Zostera noltii*, *Halodule wrightii* and *Cymodocea nodosa* that are inhabited by the lucinid bivalve *Loripes lacteus* (30). In total, we sampled 110 stations across seven intertidal flats. *Loripes* was sampled up to a depth of 20 cm using a cylindrical 15-cm diameter PVC core sampler and seagrass was sampled with a 7-cm diameter corer. Each sample was sieved over a 1-mm mesh sieve. Next, *Loripes* was counted and seagrass biomass was determined after drying for 24-h at 70 °C. Prior to linear regression analysis, *Loripes* counts and seagrass dry weight from the cores were transformed with the Box-Cox procedure to achieve normality and homoscedasticity (31).

Laboratory experiment.

Organisms and sediment for the experiment were collected in Arcachon Bay (southwest France) and transported at 15 °C to the laboratory, where both species were separately acclimatized for three weeks in 100-L polyethylene tanks. *Zostera* units contained 15 cm of sediment and 20 cm of surface water; *Loripes* tanks contained 30 cm of sediment and 5 cm of surface water. We used artificial seawater (33-35 PSU Tropic Marin at 20 °C) throughout the acclimatization period and during the experiment; pH was kept at 8.1 to 8.3 by CO₂ aeration. Light period was 16 h day⁻¹; intensity at the leaf surface was 300 μmol m⁻² s⁻¹, similar to growing season conditions in the field (32). During this three-week period, we did not observe any bivalve mortality, and seagrasses exhibited healthy vegetative growth.

Experimental setup. The lower 6-cm tall sections of 40 two-compartment PVC columns (diameter 8.4 cm) were filled with anaerobic seawater (Fig. S3). These 330-ml sections contained an injection tube and were separated from their upper compartments through a porous 0.1-mm membrane. Sediment was passed through a 1-mm sieve and transferred to the upper 12-cm tall sections (surface area: 0.0055 m²). Depending on the treatment, each unit then received either 1) *Loripes*, 2) *Zostera*, 3) both *Zostera* and *Loripes*, or 4) no further treatment. Nine *Loripes* specimens were added to each *Loripes*

treatment (~ 1600 ind. m^{-2} ; mean shell length ~ 9 mm) and 5 seagrass ramets with 2 or 3 shoots (12 shoots in total) were planted in each unit containing *Zostera* (~ 2200 sh. m^{-2} ; ~ 0.12 g shoot, ~ 0.06 g rhizome and ~ 0.03 g DW root biomass per column). Each ramet contained one apical shoot to allow vegetative growth. Pilot experiments showed that this approach ensured consistent colonization of the units within the two-week adjustment period, with no detectable mortality of the plants. Densities of both species were well within reported ranges of densities in the field (up to 23000 sh. m^{-2} for *Zostera* and 3700 ind. m^{-2} for *Loripes*) (33-35).

A full factorial experiment was designed with eight treatments and five replicates per treatment. The columns were randomly placed in a 40-cm high 250-L polyethylene basin where water flow and oxygen saturation (measured with a 556 Multi Parameter Sampler, Yellow Springs Instruments) were maintained by two aquarium water pumps, and pH was kept constant (8.1-8.3) by CO_2 aeration. After setup, the units were allowed to adjust for two weeks. During this period, sulfide levels in the treatments containing *Loripes* stabilized at ~ 7 μM , while sulfide in treatments without *Loripes* increased to ~ 233 μM . Following the adjustment period, the experiment was performed for five weeks. Sulfide levels in the lower compartments of the sulfide addition treatments were increased twice a week by 3.3-ml injections of 100 mM Na_2S solution with pH adjusted to sediment conditions (pH 7.5) with HCl, while control treatments were injected with anaerobic water. Before each injection, we used 5 cm Rhizon samplers to extract 3 ml of pore water from the main root zone (top 6 cm) of each upper compartment into vacuumized 30 ml flasks containing 3 ml Sulfide Anti-Oxidation Buffer (SAOB). After each sampling, columns were re-randomized in the basin to minimize possible differences in light levels and water flow velocities between units. Sulfide concentrations were determined immediately with an ion selective silver/sulfide electrode (Thermo Scientific (USA), Orion 9416 BN; reference electrode: Orion 900200). Oxygen detection depth was measured after five weeks with an oxygen-sensitive microelectrode (Microscale Measurements, 1-mm tip). Ammonium, nitrate and total dissolved phosphorus in the sediment pore water were also measured after five weeks. We used 5 cm Rhizon samplers to extract 10 ml of pore water from the main root zone (top 6 cm) of each upper compartment into vacuumized 30 ml flasks. Ammonium and nitrate concentrations were determined colorimetrically. Ammonium was measured with salicylate (36) and nitrate was determined by sulfanilamide after reduction of nitrate to nitrite in a cadmium column (37). Dissolved phosphorus was measured on an Inductively Coupled Plasma emission spectrophotometer (ICP; Spectroflame, Spectro). Total nitrogen concentration in *Zostera* leaves was measured in freeze-dried tissues by a CNS analyzer (type NA1500; Carlo Erba Instruments, Milan, Italy) (36). Total phosphorus was measured by ICP after digestion with nitric acid (36). *Zostera* shoot, root and rhizome biomass and *Loripes* flesh were measured as dry weight after 24 h of freeze-drying. *Loripes* shell weight was measured after drying for 24 h at 70°C . *Loripes* condition was expressed as flesh/shell dry weight ratio, which is a commonly used size-and-age independent measure of fitness in bivalves (38). Sulfur contents in the *Loripes* tissues were measured on ICP, following nitric acid digestion.

Statistical analyses. Data were tested for normality prior to analysis. Sulfide data were analyzed with Repeated-Measures three-factor ANOVA. All other variables were analyzed by two- or three-factor ANOVA. All relevant and/or significant effects and

interactions are mentioned in the figure legends or supporting text. A complete overview of the statistical output for Figures 2, 3 and S4 is provided in Table S2.

Supplementary Text

Both *Zostera* and *Loripes* significantly lowered dissolved ammonium and phosphorus in the sediment pore water, while sulfide addition increased their availability (Fig. S4). Nitrate concentrations were $0.8 \pm 0.9 \mu\text{M}$ (mean \pm SD) on average with no significant differences between treatments. Mean leaf nitrogen and phosphorus content were 1.78 ± 0.26 and 0.15 ± 0.02 % dry weight respectively, which is around reported median values from the field for both (1.8 and 0.2 % DW respectively) (39). None of the treatments had any significant effect on leaf nitrogen. Leaf phosphorus content was unaffected by *Loripes*, but decreased significantly in the sulfide addition and sulfide addition with *Loripes* treatments (from 0.17 ± 0.01 to 0.13 ± 0.01 % DW; ANOVA: $F_{1,16}=29.0$, $p<0.001$). Apparently, high sulfide levels impaired phosphorus uptake by *Zostera* in the sulfide addition treatment, leading to decreased leaf phosphorus content, despite high dissolved phosphorus availability in the pore water (Fig. S4). Our pulsed sulfide addition also seemed to impair phosphorus uptake in the sulfide addition with *Loripes* treatment, which, by interacting with the reduced dissolved phosphorus pool may have limited growth of *Zostera* under our conditions (Fig. 3).

Sulfide addition resulted in a significant increase in the relative (ANOVA: $F_{1,16}=13.8$, $p=0.002$) and absolute sulfur content (ANOVA: $F_{1,16}=24.1$, $p<0.001$) in the flesh of the bivalves. Relative sulfur content was 2.0 ± 0.2 % (g:g) in the control treatments and 3.0 ± 0.9 % in the sulfide addition treatments. The total amount of sulfur stored in *Loripes* tissues per unit was 1.3 ± 0.2 mg in the control treatments and 3.0 ± 1.1 mg in the sulfide addition treatments. These results suggest that the increased sulfide availability led to increased storage of sulfur in the tissues of the bivalves, for instance as sulfur granules in the gills (19). We found no significant effects of *Zostera* on *Loripes* sulfur content.

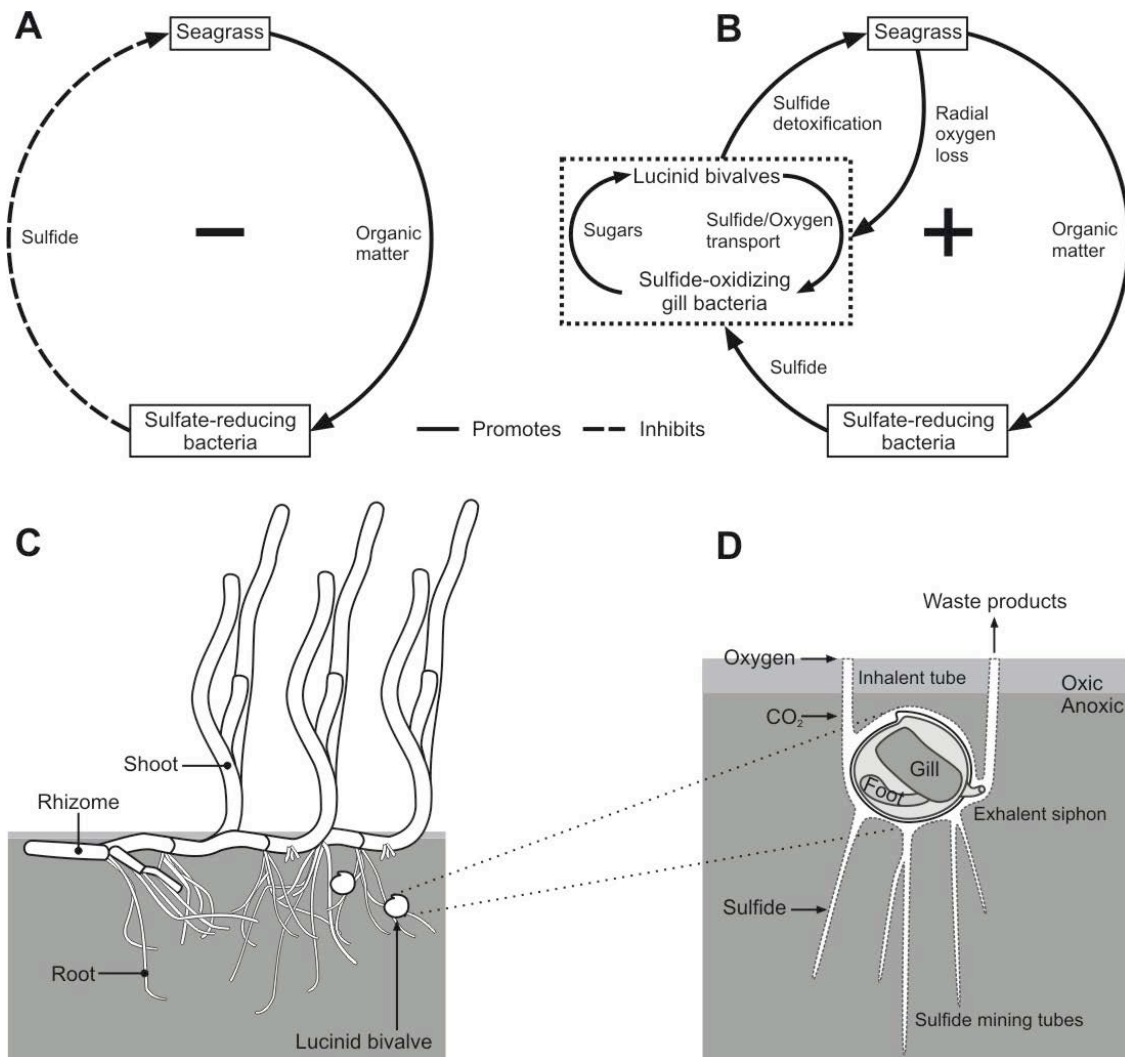


Figure S1. (A) Seagrasses generally create a negative feedback on their own growth through organic matter accumulation, which stimulates production of toxic sulfide by heterotrophic sulfate-reducing bacteria. (B) We propose in this study that the presence of lucinid bivalves and their sulfide-oxidizing gill-symbionts breaks the negative feedback, resulting in a network of positive interactions. (C) The bivalves are found in high abundances in the root zones of seagrass meadows in warmer, mild temperate to tropical regions where sulfide production rates are high. (D) They occur in the anoxic zone of the sediment and use their highly extensile foot to create tubes for sulfide mining, export of waste products and import of oxygen and CO₂ from the sediment pore water and surface water (18, 19). Both sulfide and oxygen are transported to the gills where chemoautotrophic bacteria oxidize sulfide for synthesizing sugars that fuel growth of both the bacteria and the bivalve (16-19).

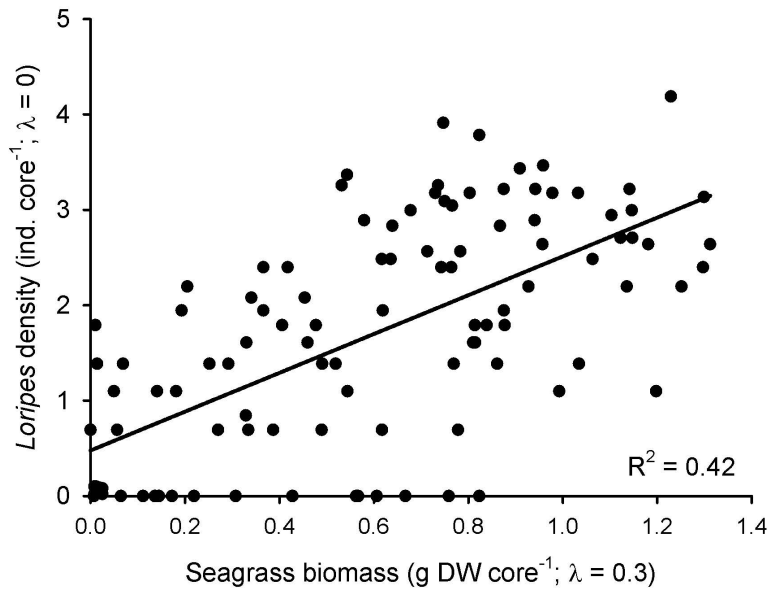


Fig. S2. Positive correlation (Pearson's $r = 0.65$) between seagrass biomass and *Loripes* density on Banc d'Arguin. *Loripes* counts and seagrass dry weight from the cores were transformed using the Box-Cox procedure prior to plotting and the regression analysis (see Materials and Methods).

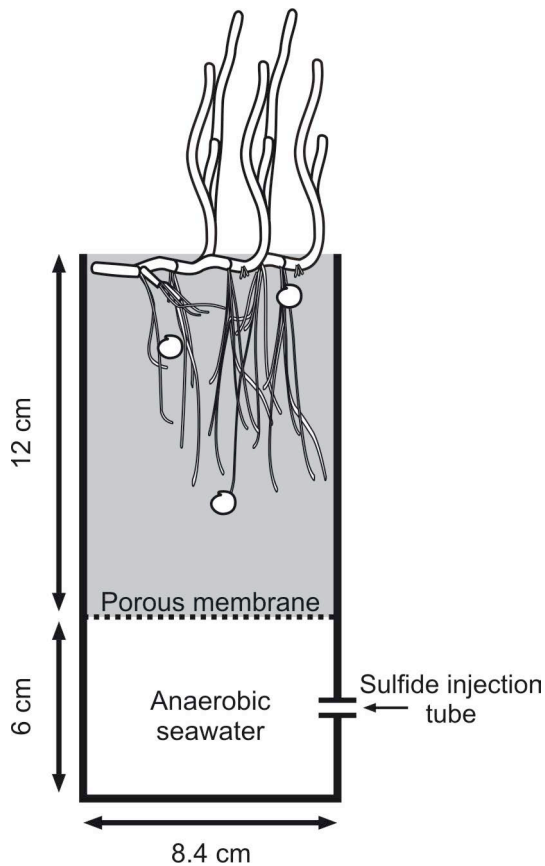


Fig. S3. Schematic drawing of the setup of an experimental unit. The dimensions of the top section were chosen to fit the organisms and to resemble field conditions. The lower section was kept large enough to allow rapid mixing and upward diffusion. Sulfide was injected twice a week in the sulfide addition treatments and allowed to diffuse from the lower compartment into the upper section through a 0.1-mm porous membrane.

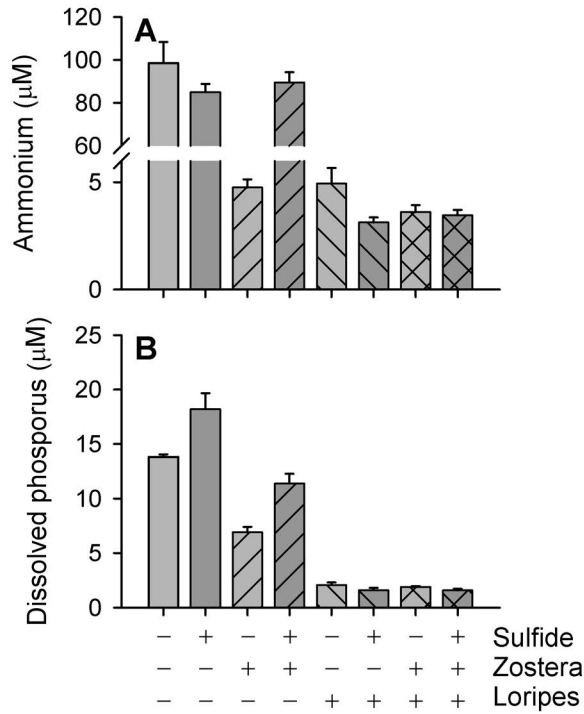


Fig. S4. Pore water ammonium and dissolved phosphorus contents after five weeks; error bars represent SEM (n=5). Ammonium (**A**) was lowered significantly by *Zostera* (ANOVA: $F_{1,32}=59.7$, $p<0.001$) and *Loripes* ($F_{1,32}=505.9$, $p<0.001$), while sulfide addition caused an increase ($F_{1,32}=35.2$, $p<0.001$). We found significant interactions between all treatments ($Z*L$: $F_{1,32}=57.1$, $p<0.001$; $Z*S$: $F_{1,32}=73.3$, $p<0.001$; $L*S$: $F_{1,32}=39.3$, $p<0.001$; $Z*L*S$: $F_{1,32}=68.5$, $p<0.001$). The treatment effects on dissolved phosphorus (**B**) were similar to ammonium, with significant effects of *Zostera* ($F_{1,32}=58.2$, $p<0.001$), *Loripes* ($F_{1,32}=562.1$, $p<0.001$) and sulfide addition ($F_{1,32}=19.6$, $p<0.001$). We found significant interactions of *Zostera* and *Loripes* ($F_{1,32}=55.1$, $p<0.001$), and *Loripes* and sulfide addition ($F_{1,32}=28.2$, $p<0.001$).

Table S1. Lucinid bivalve densities found in seagrass beds. These data provide a basic indication of the association between seagrasses and lucinids worldwide.

Area (source)	Temp.	Clim.	Seagrass genus	Lucinid genus	Density
North America					
Alaska (40, 41)	5 – 13	Temp.	<i>Zostera</i>	Lucinidae	p
Boston Harbor (42)	3 – 18	Temp.	<i>Zostera</i>		0
Chesapeake Bay (43)	1 – 23	Temp.	<i>Zostera</i>		0
Apalachee Bay, Florida (44)	18 – 29	Subtr.	<i>Syringodium, Thalassia</i>	<i>Codakia</i>	+
Biscayne Bay, Florida (45)	24 – 30	Subtr.	<i>Halodule, Syringodium, Thalassia</i>	<i>Anodontia, Codakia, Lucina</i>	++/+++
Florida Bay, Florida (18)	24 – 30	Subtr.	<i>Halodule, Syringodium, Thalassia</i>	<i>Anodontia, Codakia, Lucinesca</i>	++/+++
Indian River lag., Florida (46)	23 – 29	Subtr.	<i>Thalassia</i>	<i>Lucina</i>	p
St. Joseph's Bay, Florida (47)	18 – 29	Subtr.	<i>Thalassia</i>	<i>Lucina</i>	++/+++
Pensacola Bay, Florida (48)	18 – 29	Subtr.	<i>Halodule</i>		0
Redfish Bay, Texas (49)	19 – 29	Subtr.	<i>Halodule, Thalassia</i>	<i>Anodontia, Lucina, Phacoides</i>	p
Gulf of California, Mexico (50)	19 – 30	Subtr.	<i>Zostera, Halodule, Ruppia</i>	<i>Codakia, Divalinga</i>	p
Bahia de Chetumal, Mexico (51)	27 – 29	Trop.	<i>Syringodium, Thalassia</i>	<i>Codakia, Lucina</i>	p
Turneffe Islands, Belize, Mexico (52)	27 – 29	Trop.	<i>Thalassia</i>	<i>Codakia, Parvilucina</i>	p
Bocas del Toro, Panama (53)	27 – 29	Trop.	<i>Halodule, Syringodium, Thalassia</i>	<i>Codakia, Diplodonta Lucina, Phacoides</i>	p
Bahama's (54)	24 – 29	Trop.	<i>Thalassia</i>	<i>Codakia</i>	p
Jamaica (55, 56)	27 – 29	Trop.	<i>Thalassia</i>	<i>Anodontia, Codakia, Ctena, Divaricella, Lucina, Parvilucina</i>	+++ /++++
St Croix, Virgin Islands (57)	26 – 29	Trop.	<i>Halodule, Syringodium, Thalassia</i>	<i>Codakia, Divalinga, Lucina, Parvilucina</i>	p
Guadeloupe (58)	26 – 29	Trop.	<i>Thalassia</i>	<i>Anodontia, Codakia</i>	p
Martinique (54)	26 – 29	Trop.	<i>Thalassia</i>	<i>Lucina</i>	p
Bermuda (59, 60)	19 – 28	Subtr.	<i>Thalassia</i>	<i>Codakia, Ctena</i>	++/+++
South America					
Bahia de Neguange, Columbia (61)	26 – 29	Trop.	<i>Thalassia, Syringodium</i>	<i>Codakia, Lucina, Anodontia</i>	p
Santiago de Tolú, Columbia (62)	27 – 29	Trop.	<i>Thalassia</i>	<i>Lucina</i>	p
Morrocay, Venezuela (63)	26 – 28	Trop.	<i>Thalassia</i>	<i>Codakia</i>	+
Mochima Bay, Venezuela (64)	25 – 28	Trop.	<i>Thalassia</i>	<i>Codakia</i>	+++
Parracho de Maracajaú, Brazil (65)	26 – 28	Trop.	<i>Halophila, Halodule</i>	<i>Codakia, Divaricella</i>	p
Abrolhos Bank, Bahia Brazil (66)	25 – 28	Trop.	<i>Halodule, Halophila</i>	<i>Codakia, Ctena, Parvilucina</i>	p
Ilha do Japonês, Brazil (67, 68)	23 – 27	Trop.	<i>Halodule</i>	<i>Codakia, Divaricella</i>	++++

Table S1 (continued)

Ilha do Mel, Paranaguá, Brazil (69)	18 – 26	Trop.	<i>Halodule</i>	<i>Lucina</i>	p
Europe					
Western Atlantic, Norway (70)	6 – 13	Temp.	<i>Zostera</i>		0
Skagerrak, Atlantic, Norway (70)	4 – 17	Temp.	<i>Zostera</i>		0
Baltic, Finland (71)	1 – 16	Temp.	<i>Zostera</i>		0
Sylt, Wadden Sea (72)	4 – 18	Temp.	<i>Zostera</i>		0
South England (73)	8 – 17	Temp.	<i>Zostera</i>	<i>Lucinoma</i>	+
South Ireland (74)	9 – 17	Temp.	<i>Zostera</i>	<i>Lucinoma</i>	+++
Brittany, France (75, 76)	10 – 17	Temp.	<i>Zostera</i>	<i>Loripes</i> , <i>Lucinoma</i> , <i>Lucinella</i>	+++ /++++
Arcachon, France (77)	12 – 21	Temp.	<i>Zostera</i>	<i>Loripes</i>	++
Eo estuary, Atlantic coast, Spain (78)	13 – 19	Temp.	<i>Zostera</i>	<i>Loripes</i>	++ /+++
Mediterranean, Spain (79)	15 – 23	Subtr.	<i>Zostera</i>	<i>Lucinella</i>	+++
Mallorca, Spain (80)	14 – 25	Subtr.	<i>Posidonia</i>	<i>Ctena</i> , <i>Loripes</i> , <i>Lucinella</i>	p
Corsica, France (34)	13 – 24	Subtr.	<i>Cymodocea</i>	<i>Loripes</i>	+++ /++++
Prelo Bay, Ligurian Sea (81)	13 – 23	Subtr.	<i>Posidonia</i>	<i>Lucinella</i>	++ /+++
Venice lag., Italy (82, 83)	10 – 26	Subtr.	<i>Cymodocea</i> , <i>Zostera</i>	<i>Loripes</i>	+++ /++++
Izmir Bay, Turkey (84)	15 – 23	Subtr.	<i>Zostera</i>	<i>Loripes</i>	++
Cyprus (85)	17 – 28	Subtr.	<i>Posidonia</i>	<i>Loripes</i> , <i>Myrtea</i>	+
Black Sea, Romania (86)	6 – 24	Temp.	<i>Zostera</i>	<i>Loripes</i> , <i>Lucinella</i>	p
Africa					
Banc d'Arguin, Mauritania (35)	18 – 26	Subtr.	<i>Cymodocea</i> , <i>Halodule</i> , <i>Zostera</i>	<i>Loripes</i>	+++ /++++
Baia da Corimba, Angola (87)	22 – 29	Trop.	<i>Halodule</i>	<i>Loripes</i>	p
Kismayo, Somalia (88)	25 – 29	Trop.	<i>Halodule</i> , <i>Thalassia</i>	<i>Codakia</i> , <i>Lucina</i>	p
Zanzibar, Tanzania (89)	25 – 29	Trop.	<i>Cymodocea</i> , <i>Thalassia</i> , <i>Enhalus</i> , <i>Thalassodendron</i>	Lucinidae	++ /++++
Mahé, Seychelles (90)	26 – 30	Trop.	<i>Thalassia</i>	<i>Anodontia</i> , <i>Codakia</i> , <i>Ctena</i> ,	++
Inhaca, Mozambique (91)	23 – 27	Trop.	<i>Cymodocea</i> , <i>Halodule</i> , <i>Zostera</i>	<i>Anodontia</i> , <i>Cardiolucina</i> , <i>Loripes</i> , <i>Lucina</i> , <i>Pillucina</i>	++
Langebaan lag., South-Africa (92)	15 – 19	Subtr.	<i>Zostera</i>		0
Swartvlei estuary, South-Africa (93)	17 – 22	Subtr.	<i>Zostera</i>	<i>Loripes</i>	p

Table S1 (continued)

Asia/Pacific					
Jordan, Red Sea (94)	21 – 28	Subtr.	<i>Halodule, Halophila</i>	<i>Rasta</i>	p
Egypt, Red Sea (95)	22 – 29	Subtr.	<i>Cymodocea, Halodule, Halophila</i>	<i>Cardiolucina, Divaricella, Pillucina, Wallucina</i>	++++
United Arab Emirates (96)	21 – 33	Subtr.	<i>Halodule, Halophila</i>	<i>Anodontia, Pillucina</i>	++++
Oman (this study)	25 – 28	Trop.	<i>Halodule, Halophila</i>	<i>Pillucina</i>	++++
Palk Bay, India (97)	27 – 30	Trop.	<i>Cymodocea, Halodule, Syringodium, Thalassodendron</i>	<i>Codakia, Lucina</i>	p
Posyet Bay, Sea of Japan (98)	2 – 21	Temp.	<i>Zostera</i>	<i>Pillucina</i>	+++
Tokyo, Bay of Japan (99)	16 – 26	Subtr.	<i>Zostera</i>	Luncinidae	p
Okinawa, Japan (100)	22 – 29	Subtr.	<i>Cymodocea, Enhalus, Halodule, Halophila, Thalassia</i>	<i>Codakia, Epicodakia</i>	p
Guangxi, China (101)	20 – 29	Trop.	<i>Halodule, Halophila, Zostera</i>		0
Guangdong, China (101)	21 – 29	Trop.	<i>Halodule, Halophila</i>	<i>Pillucina</i>	p
Hainan, China (101)	22 – 29	Trop.	<i>Cymodocea, Enhalus, Halodule, Thalassia</i>	<i>Pillucina</i>	p
Tubbataha Reefs, Philippines (100)	27 – 30	Trop.	<i>Halodule, Halophila, Thalassia</i>	<i>Epicodakia</i>	p
Kungkrabaen Bay, Thailand (102)	28 – 30	Trop.	<i>Halodule</i>	<i>Anodontia, Indoaustriella, Pillucina</i>	++++
Had Chao Mai, Thailand (103)	28 – 30	Trop.	<i>Cymodocea, Enhalus, Halodule, Halophila, Thalassia</i>	<i>Pillucina</i>	++++
Pulau Semakau, Singapore (104)	28 – 29	Trop.	<i>Cymodocea, Enhalus, Halodule, Halophila, Syringodium, Thalassia</i>	<i>Anodontia</i>	p
Bone Batang, Indonesia (105)	28 – 30	Trop.	<i>Cymodocea, Enhalus, Halodule, Halophila, Thalassia</i>	Lucinidae	+++
Banten Bay, Indonesia (106)	28 – 30	Trop.	<i>Cymodocea, Enhalus, Halodule, Halophila, Syringodium, Thalassia</i>	<i>Anodontia, Codakia</i>	p
Tongapatu, Tonga (100)	23 – 27	Trop.	<i>Halodule</i>	<i>Codakia, Epicodakia</i>	p
Tarawa Atoll (107)	28 – 29	Trop.	<i>Thalassia</i>	<i>Codakia, Wallucina</i>	++/+++

Table S1 (continued)

Oceania					
Roebuck Bay, Australia (108, this study)	25 – 30	Trop.	<i>Halodule</i> , <i>Halophila</i>	<i>Anodontia</i> , <i>Ctena</i> , <i>Divaricella</i>	+++
Lizard Island, Australia (109)	25 – 29	Trop.	<i>Halophila</i>	<i>Anodontia</i> , <i>Chaviana</i> , <i>Wallucina</i>	p
Moreton Bay, Australia (109)	21 – 26	Subtr.	<i>Cymodocea</i> , <i>Halodule</i> , <i>Halophila</i> , <i>Zostera</i>	<i>Anodontia</i> , <i>Pillucina</i>	p
Rottneest Island, Australia (110)	19 – 23	Subtr.	<i>Posidonia</i>	<i>Wallucina</i>	+++ /++++
South-West Australia (111)	16 – 20	Subtr.	<i>Amphibolis</i> , <i>Posidonia</i> ,	<i>Anodontia</i>	p
New South-Wales, Australia (112)	19 – 24	Subtr.	<i>Halophila</i>	<i>Wallucina</i>	p
New South-Wales, Australia (113)	17 – 23	Subtr.	<i>Halophila</i> , <i>Zostera</i>		0
Western Port, Victoria, Australia (114, 115)	13 – 18	Temp.	<i>Halophila</i> , <i>Zostera</i>		0
Tasmania (116, 117)	12 – 16	Temp.	<i>Heterozostera</i> , <i>Ruppia</i> , <i>Zostera</i>	<i>Wallucina</i>	++ /+++
New Caledonia (118)	24 – 28	Subtr.	<i>Cymodocea</i> , <i>Halodule</i> , <i>Thalassia</i>	<i>Anodontia</i> , <i>Codakia</i> , <i>Ctena</i>	p
Slipper Island, New Zealand (119)	15 – 21	Subtr.	<i>Zostera</i>	<i>Divaricella</i>	p

Temp. depicts the mean annual temperature range based on the sea surface temperature (°C);

Clim. indicates type of climate (tropical, subtropical or temperate);

Lucinid density (spatial average): + = 1-10; ++ = 11-100; +++ = 101-1000; ++++ = >1000 ind/m²

p = present (no abundance data); u = uncertain; 0 = absent.

Table S2. Overview of the statistical output from the analyses of the data presented in Figures 2, 3, and S4.

Treatment	df	F	p
Sulfide measurements (Fig. 2A; repeated measures ANOVA)			
Zostera	1	6.8	0.014
Loripes	1	268.8	<0.001
Sulfide	1	109.7	<0.001
Zostera * Loripes	1	7.8	0.009
Zostera * Sulfide	1	2.2	0.150
Loripes * Sulfide	1	102.7	<0.001
Zostera * Loripes * Sulfide	1	2.4	0.127
Error	32		
Oxygen measurements (Fig. 2B; ANOVA)			
Zostera	1	39.3	<0.001
Loripes	1	125.0	<0.001
Sulfide	1	8.9	0.006
Zostera * Loripes	1	48.3	<0.001
Zostera * Sulfide	1	0.0	0.862
Loripes * Sulfide	1	0.3	0.578
Zostera * Loripes * Sulfide	1	0.5	0.505
Error	32		
Zostera shoot biomass (Fig. 3A; ANOVA)			
Loripes	1	61.3	<0.001
Sulfide	1	72.6	<0.001
Loripes * Sulfide	1	0.9	0.348
Error	16		
Zostera root biomass (Fig. 3B; ANOVA)			
Loripes	1	50.2	<0.001
Sulfide	1	12.0	0.003
Loripes * Sulfide	1	1.7	0.211
Error	16		
Loripes fitness (Fig. 3C; ANOVA)			
Sulfide	1	37.3	<0.001
Zostera	1	9.0	0.008
Sulfide * Zostera	1	5.4	0.034
Error	16		
Ammonium (Fig. S4A; ANOVA)			
Zostera	1	59.7	<0.001
Loripes	1	505.9	<0.001
Sulfide	1	35.2	<0.001
Zostera * Loripes	1	57.1	<0.001
Zostera * Sulfide	1	73.3	<0.001
Loripes * Sulfide	1	39.3	<0.001
Zostera * Loripes * Sulfide	1	68.5	<0.001
Error	32		
Phosphorus (Fig. S4B; ANOVA)			
Zostera	1	58.2	<0.001
Loripes	1	562.1	<0.001
Sulfide	1	19.6	<0.001
Zostera * Loripes	1	55.1	<0.001
Zostera * Sulfide	1	0.0	0.888
Loripes * Sulfide	1	28.2	0.000
Zostera * Loripes * Sulfide	1	0.0	0.965
Error	32		

References and Notes

1. M. Waycott *et al.*, Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 12377 (2009). [doi:10.1073/pnas.0905620106](https://doi.org/10.1073/pnas.0905620106) [Medline](#)
2. A. W. D. Larkum, R. J. Orth, C. M. Duarte, *Seagrasses: Biology, Ecology, and Conservation* (Springer, Berlin, 2006).
3. I. Nagelkerken, *Ecological Connectivity Among Tropical Coastal Ecosystems* (Springer Science and Business Media, Dordrecht, 2009).
4. T. van der Heide *et al.*, Positive feedbacks in seagrass ecosystems—Implications for success in conservation and restoration. *Ecosystems (N. Y.)* **10**, 1311 (2007). [doi:10.1007/s10021-007-9099-7](https://doi.org/10.1007/s10021-007-9099-7)
5. T. van der Heide, E. H. van Nes, M. M. van Katwijk, H. Olff, A. J. P. Smolders, Positive feedbacks in seagrass ecosystems—evidence from large-scale empirical data. *PLoS ONE* **6**, e16504 (2011). [doi:10.1371/journal.pone.0016504](https://doi.org/10.1371/journal.pone.0016504) [Medline](#)
6. B. B. Jørgensen, Mineralization of organic matter in the sea bed—The role of sulphate reduction. *Nature* **296**, 643 (1982). [doi:10.1038/296643a0](https://doi.org/10.1038/296643a0)
7. M. L. Calleja, N. Marba, C. M. Duarte, The relationship between seagrass (*Posidonia oceanica*) decline and sulfide porewater concentration in carbonate sediments. *Estuar. Coast. Shelf Sci.* **73**, 583 (2007). [doi:10.1016/j.ecss.2007.02.016](https://doi.org/10.1016/j.ecss.2007.02.016)
8. M. S. Koch, S. Schopmeyer, C. Kyhn-Hansen, C. J. Madden, Synergistic effects of high temperature and sulfide on tropical seagrass. *J. Exp. Mar. Biol. Ecol.* **341**, 91 (2007). [doi:10.1016/j.jembe.2006.10.004](https://doi.org/10.1016/j.jembe.2006.10.004)
9. J. D. Taylor, E. A. Glover, in *The Evolutionary Biology of the Bivalvia*, E. M. Harper, J. D. Taylor, J. A. Crame, Eds. (Geological Society of London, London, 2000), pp. 207–225.
10. L. Liljedahl, Contrasting feeding strategies in bivalves from the Silurian of Gotland. *Palaeontology* **34**, 219 (1991).
11. D. L. Distel, Evolution of chemoautotrophic endosymbioses in bivalves—Bivalve-bacteria chemosymbioses are phylogenetically diverse but morphologically similar. *Bioscience* **48**, 277 (1998). [doi:10.2307/1313354](https://doi.org/10.2307/1313354)
12. S. M. Stanley, in *Patterns of Evolution as Illustrated by the Fossil Record*, A. Hallam, Ed. (Elsevier, Amsterdam, The Netherlands, 1977), pp. 209–250.
13. J. D. Taylor, E. A. Glover, L. Smith, P. Dyal, S. T. Williams, Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). *Zool. J. Linn. Soc.* **163**, 15 (2011).
14. G. J. Vermeij, Shifting sources of productivity in the coastal marine tropics during the Cenozoic era. *Proc. R. Soc. B Biol. Sci.* **278**, 2362 (2011). [doi:10.1098/rspb.2010.2362](https://doi.org/10.1098/rspb.2010.2362) [Medline](#)
15. C. M. Cavanaugh, Symbiotic chemoautotrophic bacteria in marine invertebrates from sulphide-rich habitats. *Nature* **302**, 58 (1983). [doi:10.1038/302058a0](https://doi.org/10.1038/302058a0)

16. J. J. Childress, P. R. Girguis, The metabolic demands of endosymbiotic chemoautotrophic metabolism on host physiological capacities. *J. Exp. Biol.* **214**, 312 (2011).
[doi:10.1242/jeb.049023](https://doi.org/10.1242/jeb.049023) [Medline](#)
17. M. Johnson, M. Diouris, M. Lepennec, Endosymbiotic bacterial contribution in the carbon nutrition of *Loripes lucinalis* (Mollusca: Bivalvia). *Symbiosis* **17**, 1 (1994).
18. L. K. Reynolds, P. Berg, J. C. Zieman, Lucinid clam influence on the biogeochemistry of the seagrass *Thalassia testudinum* sediments. *Estuaries Coasts* **30**, 482 (2007).
[doi:10.1007/BF02819394](https://doi.org/10.1007/BF02819394)
19. A. E. Anderson, Metabolic responses to sulfur in lucinid bivalves. *Am. Zool.* **35**, 121 (1995).
20. Materials and methods are available as supplementary materials on *Science Online*.
21. K. Sand-Jensen, O. Pedersen, T. Binzer, J. Borum, Contrasting oxygen dynamics in the freshwater isoetid *Lobelia dortmanna* and the marine seagrass *Zostera marina*. *Ann. Bot. (Lond.)* **96**, 613 (2005). [doi:10.1093/aob/mci214](https://doi.org/10.1093/aob/mci214) [Medline](#)
22. J. M. Caffrey, W. M. Kemp, Seasonal and spatial patterns of oxygen production, respiration and root rhizome release in *Potamogeton perfoliatus* L. and *Zostera marina* L. *Aquat. Bot.* **40**, 109 (1991). [doi:10.1016/0304-3770\(91\)90090-R](https://doi.org/10.1016/0304-3770(91)90090-R)
23. M. S. Fonseca, W. J. Kenworthy, B. E. Julius, S. Shutler, S. Fluke, in *Handbook of Ecological Restoration*, M. R. Perrow, Ed. (Cambridge Univ. Press, Cambridge, 2002), pp. 149–170.
24. M. G. A. van der Heijden *et al.*, Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69 (1998). [doi:10.1038/23932](https://doi.org/10.1038/23932)
25. J. Bascompte, P. Jordano, Plant-animal mutualistic networks: The architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **38**, 567 (2007).
[doi:10.1146/annurev.ecolsys.38.091206.095818](https://doi.org/10.1146/annurev.ecolsys.38.091206.095818)
26. U. Bastolla *et al.*, The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018 (2009). [doi:10.1038/nature07950](https://doi.org/10.1038/nature07950) [Medline](#)
27. K. E. Carpenter *et al.*, One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **321**, 560 (2008). [doi:10.1126/science.1159196](https://doi.org/10.1126/science.1159196)
[Medline](#)
28. A. C. Baker, Flexibility and specificity in coral-algal symbiosis: Diversity, ecology, and biogeography of Symbiodinium. *Annu. Rev. Ecol. Evol. Syst.* **34**, 661 (2003).
[doi:10.1146/annurev.ecolsys.34.011802.132417](https://doi.org/10.1146/annurev.ecolsys.34.011802.132417)
29. NOAA/OAR/ESRL/PSD, (NOAA/OAR/ESRL/PSD, Boulder, Colorado, USA, 2011).
30. W. J. Wolff *et al.*, Biomass of macrobenthic tidal flat fauna of the Banc d'Arguin, Mauritania. *Hydrobiologia* **258**, 151 (1993). [doi:10.1007/BF00006193](https://doi.org/10.1007/BF00006193)
31. G. E. P. Box, D. R. Cox, An analysis of transformations. *J. R. Stat. Soc., B* **26**, 211 (1964).
32. M. F. Isaksen, K. Finster, Sulphate reduction in the root zone of the seagrass *Zostera noltii* on the intertidal flats of a coastal lagoon (Arcachon, France). *Mar. Ecol. Prog. Ser.* **137**, 187 (1996). [doi:10.3354/meps137187](https://doi.org/10.3354/meps137187)

33. J. E. Vermaat, F. C. A. Verhagen, Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem: Coupling demographic and physiological patterns. *Aquat. Bot.* **52**, 259 (1996). [doi:10.1016/0304-3770\(95\)00510-2](https://doi.org/10.1016/0304-3770(95)00510-2)
34. M. A. Johnson, C. Fernandez, G. Pergent, The ecological importance of an invertebrate chemoautotrophic symbiosis to phanerogam seagrass beds. *Bull. Mar. Sci.* **71**, 1343 (2002).
35. M. van der Geest, J. A. van Gils, J. van der Meer, H. Olff, T. Piersma, Suitability of calcein as an in situ growth marker in burrowing bivalves. *J. Exp. Mar. Biol. Ecol.* **399**, 1 (2011). [doi:10.1016/j.jembe.2011.01.003](https://doi.org/10.1016/j.jembe.2011.01.003)
36. L. P. M. Lamers, H. B. M. Tomassen, J. G. M. Roelofs, Sulfate-induced entrophication and phytotoxicity in freshwater wetlands. *Environ. Sci. Technol.* **32**, 199 (1998). [doi:10.1021/es970362f](https://doi.org/10.1021/es970362f)
37. E. D. Wood, F. J. A. Armstrong, F. A. Richards, Determination of nitrate in sea water by cadmium-copper reduction to nitrite. *J. Mar. Biol. Assoc. U. K.* **47**, 23 (1967). [doi:10.1017/S002531540003352X](https://doi.org/10.1017/S002531540003352X)
38. A. Lucas, P. G. Beninger, The use of physiological condition indices in marine bivalve aquaculture. *Aquaculture* **44**, 187 (1985). [doi:10.1016/0044-8486\(85\)90243-1](https://doi.org/10.1016/0044-8486(85)90243-1)
39. C. M. Duarte, Seagrass Nutrient Content. *Mar. Ecol. Prog. Ser.* **67**, 201 (1990). [doi:10.3354/meps067201](https://doi.org/10.3354/meps067201)
40. S. C. Jewett, T. A. Dean, R. O. Smith, A. Blanchard, 'Exxon Valdez' oil spill: Impacts and recovery in the soft-bottom benthic community in and adjacent to eelgrass beds. *Mar. Ecol. Prog. Ser.* **185**, 59 (1999). [doi:10.3354/meps185059](https://doi.org/10.3354/meps185059)
41. T. A. Dean, S. C. Jewett, Habitat-specific recovery of shallow subtidal communities following the Exxon Valdez oil spill. *Ecol. Appl.* **11**, 1456 (2001). [doi:10.1890/1051-0761\(2001\)011\[1456:HSROSS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1456:HSROSS]2.0.CO;2)
42. A. S. Leschen, R. K. Kessler, B. T. Estrella, *Eelgrass Restoration Used as Construction Impact Mitigation in Boston Harbor, Massachusetts* (Massachusetts Division of Marine Fisheries, New Bedford, 2009).
43. R. J. Orth, Benthic infauna of eelgrass, *Zostera marina*, beds. *Chesap. Sci.* **14**, 258 (1973). [doi:10.2307/1350754](https://doi.org/10.2307/1350754)
44. F. G. Lewis, A. W. Stoner, An examination of methods for sampling macrobenthos in seagrass meadows. *Bull. Mar. Sci.* **31**, 116 (1981).
45. H. B. Moore, L. T. Davies, T. H. Fraser, R. H. Gore, N. R. Lopez, Some biomass figures from a tidal flat in Biscayne bay, Florida. *Bull. Mar. Sci.* **18**, 261 (1968).
46. P. M. Mikkelsen, P. S. Mikkelsen, D. J. Karlen, Molluscan biodiversity in the Indian river lagoon, Florida. *Bull. Mar. Sci.* **57**, 94 (1995).
47. M. R. Fisher, S. C. Hand, Chemoautotrophic symbionts in the bivalve *Lucina floridana* from seagrass beds. *Biol. Bull.* **167**, 445 (1984). [doi:10.2307/1541289](https://doi.org/10.2307/1541289)

48. A. W. Stoner, H. S. Greening, J. D. Ryan, R. J. Livingston, Comparison of macrobenthos collected with cores and suction sampler in vegetated and unvegetated marine habitats. *Estuaries* **6**, 76 (1983). [doi:10.2307/1351809](https://doi.org/10.2307/1351809)
49. Center for Coastal Studies, *Current Status and Historical Trends of the Estuarine Living Resources Within the CCBNEP Study Area* (Center for Coastal Studies, Texas A&M University, Corpus Christi, 1996).
50. J. Torra Cosio, L. Bourillón, “Inventario y monitoreo del canal del infiernillo para el comanejo de los recursos marinos en el territorio” (SNIB- CONABIO Mexico City, 2000).
51. V. F. Quesada *et al.*, “Programa de manejo parque nacional Arrecifes de Xcalak” (Mexico National Protected Areas Commission, Mexico City, Mexico, 2004).
52. I. Hauser, W. Oschmann, E. Gischler, Modern bivalve shell assemblages on three atolls offshore Belize (Central America, Caribbean Sea). *Facies* **53**, 451 (2007). [doi:10.1007/s10347-007-0111-7](https://doi.org/10.1007/s10347-007-0111-7)
53. Continental Shelf Associates, *Synthesis of Available Biological, Geological, Chemical, Socioeconomic, and Cultural Resource Information for the South Florida Area. Supplemental Report: A Comparison of Seagrass Beds in Panama and South Florida* (U.S. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, 1995).
54. M. T. Brissac, “Nature, diversité et spécificité de l’association Lucinidae/bactéries sulfo-oxydantes” (Universite Pierre et Marie Curie Paris, 2009).
55. M. Greenway, Trophic relationship of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lytechinus variegatus* (Lamarck). *Bull. Mar. Sci.* **56**, 719 (1995).
56. J. B. C. Jackson, The ecology of the molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. *Mar. Biol.* **14**, 304 (1972). [doi:10.1007/BF00348180](https://doi.org/10.1007/BF00348180)
57. C. A. Ferguson, A. I. Miller, A sea change in Smuggler’s Cove? Detection of decadal-scale compositional transitions in the subfossil record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **254**, 418 (2007). [doi:10.1016/j.palaeo.2007.06.021](https://doi.org/10.1016/j.palaeo.2007.06.021)
58. O. Gros, M. Liberge, H. Felbeck, Interspecific infection of aposymbiotic juveniles of *Codakia orbicularis* by various tropical lucinid gill-endosymbionts. *Mar. Biol.* **142**, 57 (2003).
59. M. Aurelia, paper presented at the Seminar on organism-sediment interrelationship, Bermuda, 1969.
60. M. Schweimanns, H. Felbeck, Significance of the occurrence of chemoautotrophic bacterial endosymbionts in lucinid clams from Bermuda. *Mar. Ecol. Prog. Ser.* **24**, 113 (1985). [doi:10.3354/meps024113](https://doi.org/10.3354/meps024113)
61. J. M. Diaz, in *Las Praderas de Pastos Marinos en Colombia Estructura y Distribución de un Ecosistema Estratégico*, J. M. Díaz Merlano, L. M. Barrios Suárez, D. I. Gómez-LópezDíaz, Eds. (Instituto de Investigaciones Marinas y Costeras “José Benito Vives De Andrés” Santa Marta, Columbia, 2003), vol. 10, pp. 159.

62. A. Otero-Otero, J. Romani Lobo, “Macroinvertebrados asociados a pastos marinos (*Thalassia testudinum*) en el golfo de Morrosquillo (Zone de Berrugas) Departamento de Sucre” (Universidad de Sucre, Sincelejo, Columbia, 2009).
63. R. Bitter-Soto, Benthic communities associated to *Thalassia testudinum* (Hydrocharitaceae) at three localities of Morrocoy National Park, Venezuela. *Rev. Biol. Trop.* **47**, 443 (1999).
64. O. D. Díaz, I. Liñero-Arana, [Mollusks community associated to *Thalassia testudinum* (Bank et Köning 1805), in Mochima Bay, Venezuela]. *Acta Cient. Venez.* **55**, 44 (2004).
[Medline](#)
65. A. S. Martinez, “Distribuição e abundância da malacofauna epibentônica no parracho de Maracajaú, RN, Brasil” (Universidade federal do Rio Grande do norte centro de biociências, Natal, RN Brazil, 2008).
66. G. F. Dutra, G. R. Allen, T. Werner, S. A. McKenna, *A Rapid Marine Biodiversity Assessment of the Abrolhos Bank, Bahia, Brazil*; Rapid Assessment Program, Bulletin of Biological Assessment (Washington, USA, 2005), vol. 38, pp. 160.
67. L. V. Marques, J. C. Creed, Biologia e ecologia das Fanérogamas marinhas do Brasil. *Oecol. Bras.* **12**, 315 (2000).
68. J. C. Creed, M. Kinupp, Small-scale change in mollusk diversity along a depth gradient in a seagrass bed off Cabo Frio (Southeast Brazil). *Brazilian J. Oceanogr.* **59**, 267 (2011).
[doi:10.1590/S1679-87592011000300007](https://doi.org/10.1590/S1679-87592011000300007)
69. E. C. G. Couto, M. Savian, Caracterização sedimentológica da planície intertidal da parte sul do saco do limoeiro (Ilha do Mel - Paraná - Brasil). I. implicações ecológicas. *Braz. Arch. Biol. Technol.* **41**, 0 (1998). [doi:10.1590/S1516-89131998000200011](https://doi.org/10.1590/S1516-89131998000200011)
70. S. Fredriksen, A. De Backer, C. Bostrom, H. Christie, Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. *Mar. Biol. Res.* **6**, 189 (2010). [doi:10.1080/17451000903042461](https://doi.org/10.1080/17451000903042461)
71. C. Boström, E. Bonsdorff, Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L) beds in the northern Baltic Sea. *J. Sea Res.* **37**, 153 (1997). [doi:10.1016/S1385-1101\(96\)00007-X](https://doi.org/10.1016/S1385-1101(96)00007-X)
72. K. Reise, *Tidal Flat Ecology: An Experimental Approach to Species Interactions* (Springer-Verlag, New York, 1985), pp. 191.
73. P. R. Dando, A. J. Southward, E. C. Southward, Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proc. R. Soc. Lond. B Biol. Sci.* **227**, 227 (1986). [doi:10.1098/rspb.1986.0021](https://doi.org/10.1098/rspb.1986.0021)
74. A. L. Dale, R. McAllen, P. Whelan, *Management Considerations for Subtidal Zostera marina Beds in Ireland* (Department of Zoology, Ecology & Plant Science University College Cork, Dublin, Ireland, 2007).
75. C. Hily, M. Bouteille, Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (*Zostera marina*) (Brittany, France). *Life Sci.* **322**, 1121 (1999).
76. J. Y. Monnat, “Introduction á l’étude de la reproduction chez *Lucinoma borealis* (Linné), Bivalvia, Lucinacea” (Faculté de Science, Brest, 1970).

77. H. Blanchet, X. de Montaudouin, A. Lucas, P. Chardy, Heterogeneity of macrozoobenthic assemblages within a *Zostera noltii* seagrass bed: Diversity, abundance, biomass and structuring factors. *Estuar. Coast. Shelf Sci.* **61**, 111 (2004).
[doi:10.1016/j.ecss.2004.04.008](https://doi.org/10.1016/j.ecss.2004.04.008)
78. L. de Paz, J. M. Neto, J. C. Marques, A. J. Laborda, Response of intertidal macrobenthic communities to long term human induced changes in the Eo estuary (Asturias, Spain): implications for environmental management. *Mar. Environ. Res.* **66**, 288 (2008).
[doi:10.1016/j.marenvres.2008.04.004](https://doi.org/10.1016/j.marenvres.2008.04.004) [Medline](#)
79. J. L. Rueda, C. Salas, Molluscs associated with a subtidal *Zostera marina* L. bed in southern Spain: Linking seasonal changes of fauna and environmental variables. *Estuar. Coast. Shelf Sci.* **79**, 157 (2008). [doi:10.1016/j.ecss.2008.03.018](https://doi.org/10.1016/j.ecss.2008.03.018)
80. A. B. Centeno, “Ecología de Caulerpales: Fauna y Biomarcadores” (Mallorca, Spain, 2008).
81. A. C. Harriague, C. N. Bianchi, G. Albertelli, Soft-bottom macrobenthic community composition and biomass in a *Posidonia oceanica* meadow in the Ligurian Sea (NW Mediterranean). *Estuar. Coast. Shelf Sci.* **70**, 251 (2006). [doi:10.1016/j.ecss.2005.10.017](https://doi.org/10.1016/j.ecss.2005.10.017)
82. A. Sfriso, T. Birkemeyer, P. F. Ghatti, Benthic macrofauna changes in areas of Venice lagoon populated by seagrasses or seaweeds. *Mar. Environ. Res.* **52**, 323 (2001).
[doi:10.1016/S0141-1136\(01\)00089-7](https://doi.org/10.1016/S0141-1136(01)00089-7) [Medline](#)
83. F. Pranovi, D. Curiel, A. Rismondo, M. Marzocchi, M. Scattolin, Variations of the macrobenthic community in a seagrass transplanted area of the Lagoon of Venice. *Sci. Mar.* **64**, 303 (2000).
84. M. E. Cinar, Z. Ergen, B. Ozturk, F. Kirkim, Seasonal analysis of zoobenthos associated with a *Zostera marina* L. bed in Gulbahce Bay (Aegean Sea, Turkey). *Mar. Ecol. Pubbl. Stn. Zool. Napoli* **19**, 147 (1998).
85. M. Argyrou, A. Demetropoulos, M. Hadjichristophorou, Expansion of the macroalga *Caulerpa racemosa* and changes in softbottom macrofaunal assemblages in Moni Bay, Cyprus. *Oceanol. Acta* **22**, 517 (1999). [doi:10.1016/S0399-1784\(00\)87684-7](https://doi.org/10.1016/S0399-1784(00)87684-7)
86. S. Nicolaev, T. Zaharia, “Report on the state of the marine and coastal environment in 2010” (NIMRD, Constanta, Romania, 2011).
87. C. I. Van-Dunem do Sacramento Neto dos Santos, “Comunidades de macroninvertebrados e peixes associadas à pradaria marinha de *Hadule wrightii* (Ascherson, 1868) na Laguna do Mussulo, Angola” (Universidade de Lisboa, Lisboa, 2007).
88. G. Chelazzi, M. Vannini, Zonation of intertidal molluscs on rocky shores of southern Somalia. *Estuar. Coast. Mar. Sci.* **10**, 569 (1980). [doi:10.1016/S0302-3524\(80\)80076-4](https://doi.org/10.1016/S0302-3524(80)80076-4)
89. J. S. Eklöf, M. de la Torre-Castro, L. Adelskold, N. S. Jiddawi, N. Kautsky, Differences in macrofaunal and seagrass assemblages in seagrass beds with and without seaweed farms. *Estuar. Coast. Shelf Sci.* **63**, 385 (2005). [doi:10.1016/j.ecss.2004.11.014](https://doi.org/10.1016/j.ecss.2004.11.014)
90. J. D. Taylor, M. S. Lewis, The flora, fauna and sediments of the marine grass beds of Mahé, Seychelles. *J. Nat. Hist.* **4**, 199 (1970). [doi:10.1080/00222937000770201](https://doi.org/10.1080/00222937000770201)
91. W. F. de Boer, H. H. T. Prins, Human exploitation and benthic community structure on a tropical intertidal flat. *J. Sea Res.* **48**, 225 (2002). [doi:10.1016/S1385-1101\(02\)00160-0](https://doi.org/10.1016/S1385-1101(02)00160-0)

92. T. Siebert, G. M. Branch, Interactions between *Zostera capensis* and *Callianassa kraussi*: influences on community composition of eelgrass beds and sandflats. *Afr. J. Mar. Sci.* **27**, 357 (2005). [doi:10.2989/18142320509504095](https://doi.org/10.2989/18142320509504095)
93. A. K. Whitfield, The benthic community of the Southern Cape estuary - Structure and possible food sources. *Trans. R. Soc. S. Afr.* **47**, 159 (1989). [doi:10.1080/00359198909520160](https://doi.org/10.1080/00359198909520160)
94. J. D. Taylor, E. A. Glover, M. Zuschin, P. C. Dworschak, W. Waitzbauer, Another bivalve with dreadlocks: Living Rasta lamyi from Aqaba, Red Sea (Bivalvia: Lucinidae). *J. Conchol.* **38**, 489 (2005).
95. M. Zuschin, J. Hohenegger, Subtropical coral-reef associated sedimentary facies characterized by molluscs (Northern bay of Safaga, Red Sea, Egypt). *Facies* **38**, 229 (1998). [doi:10.1007/BF02537367](https://doi.org/10.1007/BF02537367)
96. G. R. Feulner, R. J. Hornby, Intertidal molluscs in UAE lagoons. *Tribulus (Abu Dhabi)* **16**, 17 (2006).
97. C. S. Goplinadha-Pillai, K. K. Appukuttan, Distribution of molluscs in and around the coral reefs of the southeastern coast in India. *J. Bombay Nat. Hist. Soc.* **77**, 26 (1980).
98. V. I. Kharlamenko, S. I. Kiyashko, A. B. Imbs, D. I. Vyshkvartzev, Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. *Mar. Ecol. Prog. Ser.* **220**, 103 (2001). [doi:10.3354/meps220103](https://doi.org/10.3354/meps220103)
99. N. Whanpetch, “Variability and consequences of seagrass vegetation effect on macrobenthic invertebrate communities” (Chiba University, Chiba, Japan, 2011).
100. M. Yamaguchi, in *Asian Marine Biology*, M. B., Ed. (University Press, Hong Kong 1999), vol. 15, pp. 217.
101. X. Huang, “National report on seagrass in the South China Sea–China” (South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou, China, 2008).
102. E. Meyer, B. Nilkerd, E. A. Glover, J. D. Taylor, Ecological importance of chemoautotrophic lucinid bivalves in a peri-mangrove community in eastern Thailand. *Raffles Bull. Zool.* **18**, 41 (2008).
103. M. Nakaoka, H. Mukai, S. Chunhabundit, Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed. *Ecol. Res.* **17**, 625 (2002). [doi:10.1046/j.1440-1703.2002.00520.x](https://doi.org/10.1046/j.1440-1703.2002.00520.x)
104. S. K. Tan, R. K. H. Yeo, The intertidal molluscs of Pulau Semakau: Preliminary results of “project Semakau”. *Nat. Singapore* **3**, 287 (2010).
105. J. A. Vonk, M. J. A. Christianen, J. Stapel, Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. *Estuar. Coast. Shelf Sci.* **79**, 653 (2008). [doi:10.1016/j.ecss.2008.06.002](https://doi.org/10.1016/j.ecss.2008.06.002)
106. T. E. Kuriandewa, “National report on seagrass in the South China Sea–Indonesia” (Puslit Oseanografi, Lipi, Jakarta, Indonesia, 2008).

107. G. Paulay, Benthic ecology and biota of Tarawa Atoll lagoon: Influence of equatorial upwelling, circulation and human harvest. *Atoll Res. Bull.* **487**, 1 (2000).
108. T. Piersma *et al.*, “Roebuck Bay invertebrate and bird mapping 2006” (Royal Netherlands Institute for Sea Research Texel, The Netherlands, 2006).
109. J. D. Taylor, E. A. Glover, in *Proceedings of the 13th international marine biological workshop—The Marine Fauna and Flora of Moreton Bay, Queensland*, D. P. J. F., J. A. Phillips, Eds. (Queensland Museum, South Brisbane, Australia, 2008), vol. 54, pp. 75–104.
110. P. A. G. Barnes, C. S. Hickman, in *The seagrass Flora and Fauna of Rottnest Island, Western Australia*, D. I. Walker, F. E. Wells, Eds. (Western Australian Museum, Perth, 1999), pp. 215–238.
111. P. A. Hutchings, F. E. Wells, W. D. I., G. A. Kendrick, in *The Flora and Fauna of the Albany Area, Western Australia*, W. F. E., W. D. I., H. Kirkman, R. Lethbridge, Eds. (Western Australian Museum, Perth, 1991), pp. 611–633.
112. P. J. Gibbs, G. B. Maguire, L. C. Collett, The macrobenthic fauna of *Halophila* seagrass meadows in New South Wales. *Wetlands* **4**, 23 (1984).
113. J. G. McKinnon, P. E. Gribben, A. R. Davis, D. F. Jolley, J. T. Wright, Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. *Mar. Ecol. Prog. Ser.* **380**, 59 (2009). [doi:10.3354/meps07926](https://doi.org/10.3354/meps07926)
114. G. J. Edgar, C. Shaw, G. F. Watson, L. S. Hammond, Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *J. Exp. Mar. Biol. Ecol.* **176**, 201 (1994). [doi:10.1016/0022-0981\(94\)90185-6](https://doi.org/10.1016/0022-0981(94)90185-6)
115. G. F. Watson, A. I. Robertson, M. J. Littlejohn, Invertebrate macrobenthos of the seagrass communities in Western Port, Victoria. *Aquat. Bot.* **18**, 175 (1984). [doi:10.1016/0304-3770\(84\)90086-X](https://doi.org/10.1016/0304-3770(84)90086-X)
116. G. J. Edgar, N. S. Barrett, D. J. Gradon, “A classification of Tasmanian estuaries and assessment of their conservation significance using ecological and physical attributes, population and land use” (Published by the Marine Research Laboratories, University of Tasmania Tasmania, 1999).
117. G. J. Edgar, N. S. Barrett, P. R. Last, The distribution of macroinvertebrates and fishes in Tasmanian estuaries. *J. Biogeogr.* **26**, 1169 (1999). [doi:10.1046/j.1365-2699.1999.00365.x](https://doi.org/10.1046/j.1365-2699.1999.00365.x)
118. E. A. Glover, J. D. Taylor, Diversity of chemosymbiotic bivalves on coral reefs: Lucinidae (Mollusca, Bivalvia) of New Caledonia and Lifou. *Zoosystema* **29**, 109 (2007).
119. A. M. Schwarz, M. Morrison, I. Hawes, J. Halladay, Physical and biological characteristics of a rare marine habitat: sub-tidal seagrass beds of offshore islands. *Sci. Conserv.* **269**, 5 (2006).